Pedobiologia, Bd. **13**, S. 90—98 (1973)

Graduate Program in Ecology The University of Tennessee and
Environmental Sciences Division Oak Ridge National Laboratory

# Exploitation of deciduous leaf litter by *Apheloria montana* (Diplopoda: Eurydesmidae)

J. F. McBrayer

With 2 figures

(Accepted 1. X. 1972)

## List of Contents

1. Introduction . . . . . 90
2. Methods and materials . . . . . 91
2.1. Rearing methods; 2.2. Energetics and microbial analysis; 2.3. Elemental analysis
3. Results and discussion . . . . . 93
3.1. Energetics; 3.2. Elemental balances
4. Conclusions . . . . . 96
5. Acknowledgements . . . . . 97
6. Summary . Zusammenfassung . . . . . 97
7. Literature cited . . . . . 97

## 1. Introduction

The importance of litter decomposition in temperate forests is axiomatic, yet this process remains poorly understood. The process has been conceptualized (e. g., Pochon et al 1969) as a synergestic relationship, between various invertebrates and the microflora, which accelerates litter disappearance while depressing the rate of nutrient release. For example, Engelmann (1961) suggested that the production efficiency of litter fungi was maximized by fungivores whose grazing maintained fungal populations in irruptive growth phases. Other studies have illustrated increased decomposition rates resulting from a temporary shift in microbial populations, from fungi to bacteria, as a consequence of litter passage through the guts of millipedes (Nicholson et al. 1966) or caddis fly larvae (van der Drift and Witkamp 1960). In any case, efficient utilization of forest litter appears to be contingent upon an initial litter fragmentation which alters the microbial substrate both physically and chemically. The unresolved question is how the fragmenters maintain viable populations on litter which is intrinsically low in readily available energy and essential ions.

Availability of energy is a consequence of the chemical form of carbon in the food source and the congruity of the consumer digestive enzyme system. Burges (1967) reported C/N ratios for fresh litter ranging from about 20 : 1 to 50 : 1. Much of that

Contribution No. 53 from the Eastern Deciduous Forest Biome, US-IBP, funded by the National Science Foundation under Interagency Agreement AG-199, 40-193-69 with the Atomic Energy Commission — Oak Ridge National Laboratory.

carbon occurs in cellulose, which not only is inaccessible to most metazoa (NIELSEN 1962), but may physically interfere with the utilization of other compounds. Indirect methods of dealing with cellulose rich diets are commonplace. The rumen of many large mammals and the gastric caeca of wood-boring insects represent one evolutionary approach, i. e., the provision of a pouch housing unicellular symbionts which contribute the lacking cellulases. Earthworms, through geometry and slow gut turnover allow for a similar mechanism within the mainstream of the gut (SATCHELL 1967). Coprophagy, in the sense of ingesting feces of the same or a trophically similar species, can accomplish the same end in animals lacking such morphological adaptation. Coprophagy is well known in lagomorphs and rodents (e. g., BOURLIERE 1954), isopods (WIESER 1966) and xylophagous beetles (MASON and ODUM 1969). Although the results of coprophagy and gut symbionts are similar, the rates at which these processes occur are not necessarily the same. BURNETT et al. (1969) demonstrated that the ability to utilize wood was essentially the same in a roach with caecal symbionts and a coprophagous beetle. The roach, however, excreted a radioactive tag ($^{65}Zn$) significantly faster ($P < 0.05$). Using a radioactive tag ($^{137}Cs$) to discern trophic structure in a cryptozoan food-web, MCBRAYER and REICHLE (1971) identified millipedes as primary litter fragmenters and speculated that coprophagy was the likely method of exploitation. This study was begun to determine

1) if the millipedes in question were, in fact, coprophagous
2) if coprophagy is essential to their normal functioning, and
3) how coprophagy affects energy utilization and elemental turnover.

## 2. Methods and materials

### 2.1. Rearing methods

*Apheloria montana* (BOLLMAN) were collected from a mesic hardwood forest on the U. S. Atomic Energy Commission Reservation at Oak Ridge, Tennessee, during late summer 1970. *A. montana* is a large (up to ca. 1.0 g dry wt.) eurydesmid millipede apparently endemic to eastern Tennessee (CHAMBERLIN and HOFFMAN 1958). The genus, with some twenty species, is found throughout most of the eastern United States. On the Oak Ridge Reservation, *A. montana* forms an important component of the litter stratum with dry biomass often exceeding that of the total litter mesofauna (REICHLE, unpublished data).

Millipedes were brought into a controlled environment facility and maintained on leaf litter at 21 °C and 75% relative humidity under a 14-hour light — 10-hour dark illumination program. After an acclimation period of > 30 days, the millipedes were placed singly into 13.3 cm × 12.7 cm × 3.4 cm deep plastic culture chambers (Fig. 1) and maintained under the same environmental conditions. A free-water source, consisting of a synthetic polymer sponge fitted to a water-filled vial, was necessary for successful rearing. Each culture chamber was provided with a gravity-fed litter dispenser designed to permit free access for feeding while preventing contamination with feces. Litter dispensers contained 2.2 ± 0.1 (standard error) g dry wt. litter. Litter was ground to pass a 2 mm mesh, in order to permit use of the dispensers, and was tagged, by soaking, with 12 $\mu$Ci $^{137}Cs$ $g^{-1}$ litter.

Ten millipedes were randomly selected for the control group, i. e., with access to their own feces. Another ten were deprived of their feces by placing a 6 mm wire mesh 6 mm above the floor of the chamber (Fig. 1). Any feces deposited on the wall of the chamber or on the water source were removed daily.

### 2.2. Energetics and microbial analysis

A daily energy budget (cal $g^{-1}$ dry wt.) at 21 °C was constructed in the form of

$$\text{Ingestion } (I) = \text{Assimilation } (A) + \text{Excretion } (E) \quad (1)$$

where assimilation is the sum of production (P) and respiration (R). Ingestion was calculated as the calorific equivalent of litter consumed. Production was determined as the calorific equivalent of the change in dry weight over the period of the experiment, assuming a constant growth rate. Respiration was determined directly and converted to calories using a laboratory determined respiration quotient of 0.82. Excretion was calculated from equation (1).

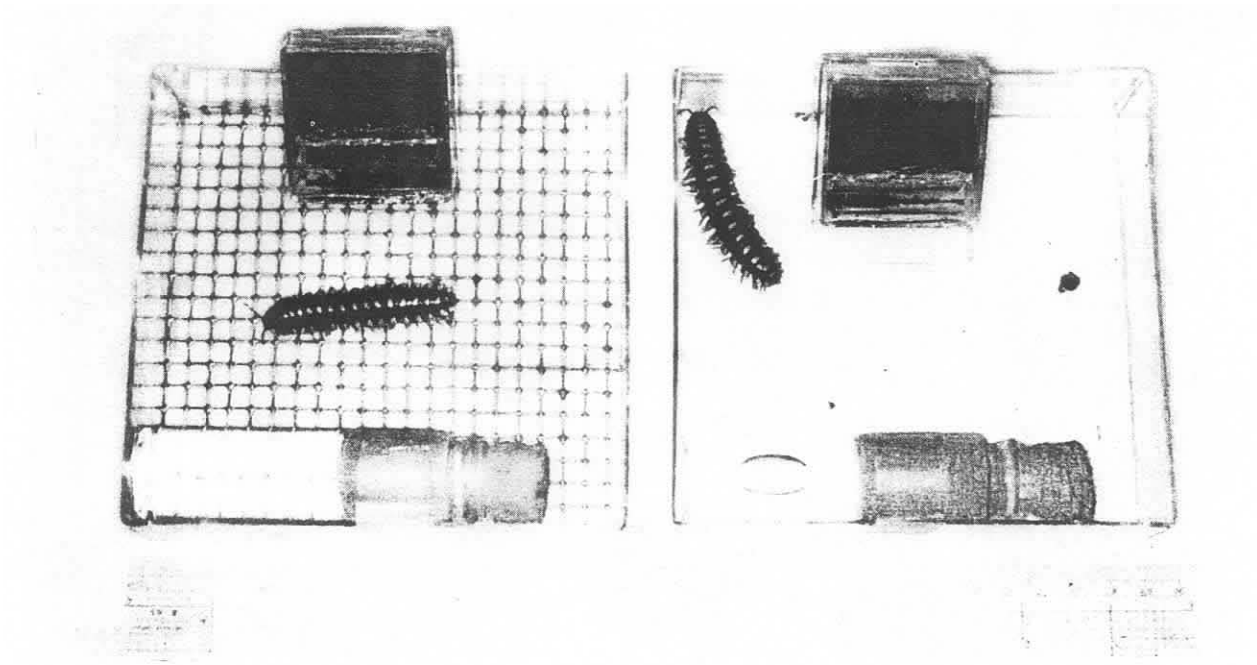

Fig. 1 *Apheloria montana* in rearing cages. Wire mesh in cage at left allowed faces to drop through, preventing the millipede from ingesting its own feces.

All calorific determinations were made using a Parr adiabatic bomb calorimeter. Samples were prepared by drying at 40 °C for one week to avoid loss of volatile waxes and oils (Southwood 1966). Each determination was based on three replicate samples. Respiration was measured on a Gilson differential respirometer using 0.1 N KOH as the $CO_2$ absorbent. Although measurements were taken at 21 °C, the same temperature as culture conditions, animals were allowed to adjust to the confined space of the respirometer flasks for 30 minutes before measurements were initiated.

Bacterial and fungal colony counts were performed on both litter and feces by the pour plate method. Litter samples were taken from the same material used in millipede cultures and feces were freshly collected from millipedes used in the experiment (the "deprived" or experimental group). Fungal counts were obtained from aqueous suspensions at dilutions of $10^{-3}$ (mg dry wt. $ml^{-1}$) on Difco Sabouraud maltose agar (*p*H 5.6 at 25 °C). Bacterial counts were obtained from aqueous suspensions at dilutions of $10^{-5}$ (mg dry wt. $ml^{-1}$) on Difco nutrient agar (*p*H 6.8 at 25 °C). Four replicates of each culture were established and counts were taken after incubation at 30 °C for 48 hours. Two water blanks on each substrate demonstrated no external contamination.

## 2.3. Elemental analysis

Millipedes were counted for gamma emissions on a Packard Auto-Gamma Spectrometer equipped with a 7.6 cm diameter Tl-activated NaI well-crystal. All counts were standardized and expressed as pCi $mg^{-1}$ dry wt., corrected for mean weight increments for each group. Constant geometry was maintained, and desiccation avoided, during counting by sandwiching millipedes between wetted sponge plugs at a constant level within the counting tubes. Twice background was arbitrarily set as the minimum acceptable net counting rate. All millipedes attained that count rate by the first day post-tagging. Millipedes were counted daily for the first week, once mid-way through the experiment and at the end of the experiment (day 32, post-tagging). Although neither group reached equilibrium with their food base, concurrent analyses showed that these data were sufficient to estimate equilibrium with a standard error of the estimate of less than 10 %. The parameters of interest, the rate at which the radionuclide was accumulated ($\lambda$) and the body burden at equilibrium ($Q_e$) were estimated by fitting nonlinear least squares regressions to the data, in the form of:

$$Q_t = Q_e(1 - e^{-\lambda t})$$

where $Q_t$ = radioactivity concentration, in pCi mg$^{-1}$, at any time, $t$; $Q_e$ = radioactivity concentration when at equilbrium with the food-base; $e$ = base of natural logarithms; $\lambda$ = the rate of radionuclide accumulation, day$^{-1}$; and, $t$ = time elapsed, days, since feeding on radioactive food was initiated.

Millipedes, litter and feces were analyzed for sodium, potassium and calcium using a Coleman Model 21 Flame Photometer. Samples were dried, as in preparation for calorimetry, ground to a powder and redried overnight. Three replicates of ca. 2.5 g of each material were ashed in a muffle furnace at 450 °C for 24 hours. Ashed samples were cooled in desiccators over $CaCl_2$ before weighng. Ash residues were washed into acid-clean glassware with 0.1 N HCl, taken into solution with 4.0 N HCl and evaporated to near dryness. After cooling, the samples were treated with 5 m$l$ of 30% $H_2O_2$ to assure complete digestion of any remaining organic matter. After allowing ca. 30 minutes for the peroxide to react, the samples were again evaporated to near dryness. The residue was then washed through Whatman No. 42 filter paper with 0.1 N HCl to remove undissolved silicates and the filtrate was brought to 100 m$l$ with distilled water.

Preliminary analyses were performed to estimate concentrations and samples were diluted to yield ca. 1—3 ppm on final analysis. This range gave a linear calibration curve from 0 to 5 ppm for each of the elements. In order to avoid interference from sulfate and phosphate ions, samples for calcium analysis and blanks were burned with 50% 1000 ppm $La_2O_3$ (YOFE and FINKLESTEIN 1958).

## 3. Results and discussion

### 3.1. Energetics

That coprophagy plays a role in the energetics of *A. montana* is evident from Table 1. By weighing the litter remaining at the end of the experiment, mean litter ingestion rates ($I$) were determined: 66.1 mg dry wt. litter g$^{-1}$ dry wt. millipede day$^{-1}$ for the experimental group (deprived of feces) versus 28.7 mg g$^{-1}$ day$^{-1}$ for controls. At 3.9 $\pm$ 0.03 (S. E.) cal mg$^{-1}$ dry wt. litter, this represents an increase of about 145 cal g$^{-1}$ millipede day$^{-1}$, or more than double the normal ingestion rate.

The weight specific calorific equivalents of the two groups were not significantly different, 1.75 $\pm$ 0.01 cal mg$^{-1}$ for experimentals and 1.76 $\pm$ 0.01 cal mg$^{-1}$ for controls, but were not averaged for subsequent calculations. Weight increment was equated with total net production ($P$), because of isolation of individuals, and amounted to 1.1 cal g$^{-1}$ day$^{-1}$ for the experimental group and 3.8 cal g$^{-1}$ day$^{-1}$ for controls. Respiration ($R$) accounted for 12.2 and 13.5 cal g$^{-1}$ day$^{-1}$, respectively. Thus, total assimilation ($A = P + R$) amounted to 13.3 cal g$^{-1}$ day$^{-1}$ for millipedes deprived of their feces and 17.3 cal g$^{-1}$ day$^{-1}$ for controls.

To deprive millipedes totally of feces proved impossible. It was assumed, however, that any feces ingestion by the deprived group was negligible. Also, the turn around time would have been sufficiently short as to prohibit significant microbial activity. Consequently, any feces ingested could be considered homologous to litter. With these assumptions, assimilation efficiency ($AE = A/I$) for litter was calculated at 0.052. It was also assumed there was no difference in assimilation efficiency for litter between the two

Table 1 Effect of coprophagy on the energetics of *Apheloria montana* at 21 °C

| | Energy flux (cal g$^{-1}$ day$^{-1}$) | |
|---|---|---|
| | Litter plus Feces | Litter only |
| Litter ingestion | 111.3 | 256.7 |
| Feces ingestion | 105.5 | — |
| Total ingestion | **216.8** | **256.7** |
| Production | 3.8 | 1.1 |
| Respiration | 13.5 | 12.2 |
| Total assimilation | **17.3** | **13.3** |
| Primary egestion | 105.5 | 243.4 |
| Net egestion | **94.0** | **243.4** |

groups. At $AE = 0.052$, the control group was estimated to assimilate 5.7 cal $g^{-1}$ $day^{-1}$ from the initial passage of litter. Total assimilation was calculated to be 17.3 cal $g^{-1}$ $day^{-1}$, which left 11.6 cal $g^{-1}$ $day^{-1}$ derived from feces.

To appreciate the role of coprophagy in litter exploitation, it is necessary to know the extent to which the assimilation efficiency for feces differs from that for litter. The most direct method would be:

$$AE \text{ for feces} = \frac{\text{calories assimilated from feces}}{\text{calories ingested as feces}}$$

The nature of the experiment obviated this approach. If we assume each day's primary fecal production (unassimilated litter from first passage) is ingested, 11.6 cal $g^{-1}$ $day^{-1}$ assimilated, $AE$ for feces becomes 0.138 and final elimination becomes 94.0 cal $g^{-1}$ $day^{-1}$. By combining calories ingested from litter and feces and dividing into total assimilation, a net assimilation efficiency of 0.080 is derived. This figure is quite compatible with those of Bocock (1963), who reported net assimilation efficiencies (dry matter) of 0.06 to 0.105 for the millipede *Glomeris* sp., with an average efficiency of ca. 0.08. Consequently, reingestion of all first passage fecal matter appears well within reason, although it may not be attained under field conditions.

Obviously, the materials least resistant to the millipede enzyme systems are the first to be extracted from litter. The increased assimilation due to coprophagy is, therefore, more complex than a simple second attack on the material. The process can be surmised from the data presented in Table 2. Although the litter was ground in order to permit the use of gravity-flow feeders, mean particle size was further decreased from 0.24 to 0.04 $mm^2$ with the concomitant increase in surface area. An increase in $p$H from 5.5 in itter to 7.7 in feces was accompanied by an eightfold increase in moisture. Increased

Table 2 Effect of gut passage by *Apheloria montana* on some physical, chemical and biological properties of litter

| | Particle Size ($mm^2$) | $p$H | Moisture (% Dry Wt.) | Kcal $g^{-1}$ (Dry Wt.) | Colonies $g^{-1}$ Dry Wt. | |
|---|---|---|---|---|---|---|
| | | | | | Fungi ($\times 10^4$) | Bacteria ($\times 10^6$) |
| Litter | 0.24 | 5.5 | 49.6 | 3.88 | 49 ± 5 | 76 ± 10 |
| Feces | 0.04 | 7.7 | 392.0 | 3.45 | 1 ± 0.2 | 116 ± 6 |

moisture and surface area both favor increased microbial activity. The increase in $p$H gives bacteria a competitive advantage over fungi and thus further accelerates the potential decomposition rate. These results are similar to those obtained by van der Drift and Witkamp (1960) for larvae of the terrestrial caddis fly *Enoicyla pusilla* Burm. They also reported that the fecal pellets had greater water holding capacity than the original litter, a phenomenon which would further sustain microbial activity, and exhibited a temporal decline in cellulose content. Thus, bacterial activity in the fecal pellet results in an increase in matter extractable by the millipede on subsequent reingestion, namely, bacterial biomass and digestion products.

### 3.2. Elemental balances

Sodium, potassium and calcium are considered "biologically determinant" elements, i. e., their levels within organisms are determined by species physiology and are relatively independent of environmental levels (Reichle and van Hook, in press). Levels for the elements in forest litter, millipedes and millipede feces are shown in Table 3. The

Table 3 Content of sodium, potassium and calcium in millipedes, forest litter and millipede feces

| | % Ash ± S. E. | mg $g^{-1}$ Ash ± S. E. | | |
|---|---|---|---|---|
| | | Na | K | Ca |
| Millipedes Deprived of Feces | 49.9 ± 0.4 | 3.8 ± 0.03 | 12.0 ± 0.4 | 462.4 ± 27.4 |
| Millipedes with Access to Feces | 48.5 ± 0.4 | 4.1 ± 0.02 | 12.6 ± 0.4 | 419.0 ± 16.1 |
| Litter | 52.8 ± 0.4 | 1.2 ± 0.01 | 4.8 ± 0.1 | 49.9 ± 0.7 |
| Feces | 27.9 ± 1.0 | 0.8 ± 0.02 | 5.6 ± 0.1 | 226.6 ± 11.1 |

Table 4 Effect of coprophagy on assimilation and total uptake of sodium, potassium and calcium by *Apheloria montana* at 21 °C

| Element | Litter Diet Only | Litter Plus Feces |
|---|---|---|
| Sodium (Na) | | |
| *Assimilation* (%) | 3.3 | 13.1 |
| Total uptake (mg $g^{-1}$ $day^{-1}$) | 0.15 | 0.13 |
| Potassium (K) | | |
| *Assimilation* (%) | 2.6 | 7.5 |
| Total uptake (mg $g^{-1}$ $day^{-1}$) | 0.59 | 0.71 |
| Calcium (Ca) | | |
| *Assimilation* (%) | 8.3 | 9.8 |
| Total uptake (mg $g^{-1}$ $day^{-1}$) | 6.25 | 21.15 |

differences between millipedes were not significant. Elemental differences between litter and feces were highly significant ($P < 0.01$).

Lack of differences in elemental content between millipedes with and without access to their feces does not necessarily indicate that coprohagy has no effect on elemental assimilation. Table 4 expresses daily elemental increments (assuming elemental contents to remain constant with growth) as percent of element ingested and as a proportion of body dry weight. The former represents an approximate assimilation rate and the latter is a measure of total element assimilated. With both sodium and potassium, coprophagy increased assimilation. The increased ingestion rate in the experimental group, however, apparently offset the difference in assimilation efficiencies. In contrast to cesium, the levels of sodium and potassium were relatively unaffected by the forced change in diet. Calcium comprised almost half of the ash residues in *A. montana* (Table 3), a consequence of the calcareous matrix of the exoskeleton (Reichle et al. 1969). The assimilation efficiencies for calcium were similar; the greater total uptake in the control group resulted primarily from increased growth.

The effect of a coprophagous habit on the kinetics of a radioactive food-tag is illustrated in Fig. 2. The rate at which radioactive ions are accumulated ($\lambda$) is a complicated function which is related to feeding rate, assimilation efficiency for the radionuclide, and excretion rate, among others. The equilibrium concentration ($Q_e$) is proportional to the concentration of $^{137}Cs$ in the food source. The parameter $Q_e$ is an important criterion in delineating trophic relationships (e. g., McBrayer and Reichle 1971).

For millipedes with access to feces (Fig. 2, solid line), $\lambda = 0.0484$ $day^{-1}$ and the millipedes attained 95% of $Q_e$ on day 62, post-tagging. Millipedes deprived of feces (broken

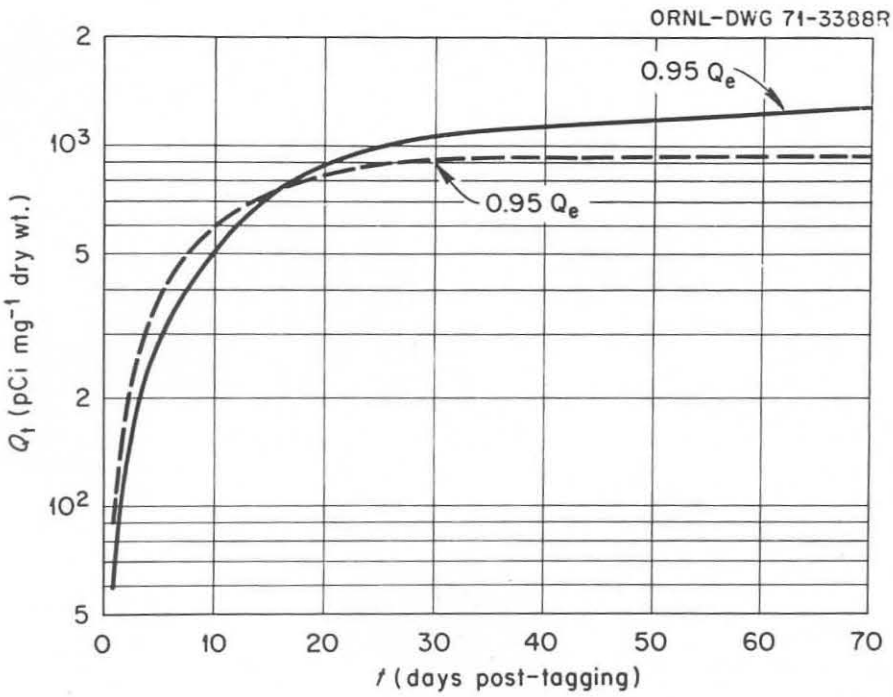


Fig. 2 Uptake of cesium-137 at 21 °C by *Apheloria montana*. The uptake rate for millipedes deprived of feces (broken line) was 0.0997 day$^{-1}$ versus 0.0484 day$^{-1}$ for controls (solid line).

line) accumulated cesium twice as rapidly as the controls ($\lambda = 0.0997$ day$^{-1}$) because of the increased ingestion rate. Equilibrium was approached more rapidly, but at a lower level (945 pCi mg$^{-1}$ versus 1338 pCi mg$^{-1}$). Coprophagy resulted in greater assimilation of the radionuclide.

## 4. Conclusions

Although *Apheloria montana* feeds on leaf litter, that diet alone has been shown to be insufficient. This implies that *A. montana* does not rely on internal symbionts to process food material. The fact that coprophagy represents a workable solution to the cellulose-rich food base is evident from a comparison of production figures. Production as calories added (Table 1) indicates almost a 3.5 : 1 advantage accruing to millipedes with access to their own feces. Calories added, however, is only one aspect of production. Reference to Table 3 provides the information that these organisms are nearly 50% ash and that ca. 90% of the ash is calcium, which is localized in the exoskeleton. Consequently, there may be little correlation between increments in heat equivalency and dry biomass. The millipedes with access to feces increased body dry weight by ca. 16% in 30 days compared to $< 1\%$ in millipedes deprived of feces.

By the twenty-first day of the experiment, millipedes deprived of feces began to cease fecal production and to become inactive. Within a week, two from this group had died and another three had suffered weight losses up to ca. 10%. The experiment was therefore terminated on day 32. Obviously, coprophagy was essential to the very survival of the millipedes.

Although this work focused on the ability of millipedes to process cellulose, a number of additional, uninvestigated possibilities exist.The high C/N ratios in fresh litter are as indicative of low nitrogen content as they are of high cellulose. The possibility of bacterial fixation of nitrogen in millipede feces may be of major importance. The cations investigated did not appear to be limiting. Where significant differences in elemental assimilation efficiencies occurred (sodium and potassium), increased ingestion by the experimental group offset these differences.

A final point concerns the role of fragmenters as regulators of the decomposition process. Modifications to the substrate, which lead to increased bacterial activity, yield increased litter decomposition rates. The incorporation of breakdown products into living biomass, both in fragmenters and microflora, tends to dampen fluctuations in elemental release. Thus these organisms may be important stabilizers of nutrient cycles.

## 5. Acknowledgements

The author expresses his gratitude to Drs. D. E. Reichle and R. I. van Hook, Jr., Oak Ridge National Laboratory, for their many helpful discussions. Drs. R. V. O'Neill and M. Witkamp thoughtfully criticized the manuscript. Dr. S. I. Auerbach, Director, Environmental Sciences Division, ORNL, made available the facilities under his direction, for which the author is most grateful. During part of this study, the author was supported by a National Aeronautic and Space Administration grant to the Graduate Program in Ecology, The University of Tennessee.

## 6. Summary · Zusammenfassung

[Verwertung von Fallaub durch *Apheloria montana*]

*Apheloria montana* (Bollmann) ist eine von den Invertebraten-Arten, die eine beschleunigte Waldstreuzersetzung verursacht, indem sie die Eignung der Streu als Substrat für mikrobielle Prozesse erhöht. *A. montana* scheinen jedoch Zellulase produzierende Symbionten zu fehlen, die gewöhnlicherweise mit Wirbellosen assoziiert sind und die den Zelluloseabbau besorgen. Die Diplopoden verwerten die Streu durch Koprophagie, in einer Art, die als „externer Rumen" bezeichnet wurde. Die mikrobielle Aktivität wurde durch die Darmpassage stimuliert, der eigentliche Abbau erfolgt extern; die Diplopoden fressen ihre eigene Faezes und nutzen so den Vorteil der bakteriellen Zellulasen. Diplopoden, denen im Experiment die Faezes zugänglich waren nahmen in 30 Tagen 16% ihres Trockengewichts zu im Vergleich mit 1% Gewichtszunahme von Tieren, denen die Faezes entzogen wurden. Die Diplopoden [dieser Art] enthalten annähernd 50% Aschebestandteile; davon sind 90% Calcium, das im Außenskelett enthalten ist. Folglich mag eine geringe Korrelation zwischen der Zunahme der Biomasse in Kalorien und der Trockengewichtszunahme bestehen.

## 7. Literature cited

Bocock, K. L., 1963. The digestion and assimilation of food by *Glomeris*. pp. 85–91, In: J. Doeksen and J. van der Drift (eds.): Soil Organisms. Amsterdam, North-Holland Publ. Co.

Bourliere, F., 1954. The natural history of mammals. New York, Alfred A. Knopf.

Burges, A., 1967. The decomposition of organic matter in soil. pp. 479–492. In: A. Burges and F. Raw (eds.): Soil Biology. London and New York, Academic Press.

Burnett, A. M., W. H. Mason and S. T. Rhodes, 1969. Reingestion of feces and excretion rates of $^{65}$Zn in *Popilius disjunctus* versus *Cryptocercus punctulates*. Ecol. **50**, 1094–1096.

Chamberlin, R. V., and R. L. Hoffman, 1958. Checklist of millipedes of North America. U. S. National Museum Bull. 212. Washington, Smithsonian Institution.

Engelmann, M. D., 1961. The role of soil arthropods in the energetics of an old field community. Ecol. Monogr. **31**, 221–238.

Mason, W. H., and E. P. Odum, 1969. The effect of coprophagy on retention and bioelimination of radionuclides by detritus-feeding animals. pp. 721–724, In: D. J. Nelson and F. C. Evans (eds.): Symposium on Radioecology. U. S. AEC CONF-670503 (T1D-4500).

McBrayer, J. F., and D. E. Reichle, 1971. Trophic structure and feeding rates of forest soil invertebrate populations. Oikos **22**, 381–388.

Nicholson, P. B., K. L. Bocock and O. W. Heal, 1966. Studies on the decomposition of the faecal pellets of a millipede [*Glomeris marginata* (Villers)]. J. Ecol. **54**, 755–766.

Nielsen, C. O., 1962. Carbohydrases in soil and litter invertebrates. Oikos **13**, 200–215.

Pochon, J., P. Tardieux and J. d'Aguilar, 1969. Methodological problems in soil biology. pp. 13–63, In: Soil biology, reviews of research. Paris, UNESCO.

Reichle, D. E., M. H. Shanks and D. A. Crossley, Jr., 1969. Calcium, potassium and sodium content of forest floor arthropods. Ann. Entomol. Soc. Amer. **62**, 57–62.

Reichle, D. E., and R. I. van Hook, Jr., 1970. Radionuclide dynamics in insect food chains Can. Entomol. **4**, 22—32.

Satchell, J. E., 1967. Lumbricidae. pp. 259–322, In: A. Burges and F. Raw (eds.): Soil biology. London and New York, Academic Press.
Southwood, T. R. E., 1966. Ecological methods, with particular reference to the study of insect populations. London, Methuen.
Van der Drift, J., and M. Witkamp, 1960. The significance of the break-down of oak litter by *Enoicyla pusilla* Burm. Arch. Neerl. Zool. **13**, 486–492.
Wieser, W., 1966. Copper and the role of isopods in degradation of organic matter. Science **153**, 67–69.
Yofe, J., and R. Finkelstein, 1958. Elimination of anionic interference in flame photometric determination of calcium in the presence of phosphate and sulfate. Anal. Chim. Acta **19**, 166–173.

Address of the author: J. F. McBrayer, Environmental Biology Division, Laboratory of Nuclear Medicine and Radiation Biology, University of California, Los Angeles, California 90024, U.S.A.